

The University of Chicago

NEW LEPIDOSTROBI
FROM CENTRAL UNITED STATES

A DISSERTATION SUBMITTED TO THE
FACULTY OF THE DIVISION OF THE BIO-
LOGICAL SCIENCES IN CANDIDACY FOR
THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF BOTANY

1939

By

GREGORY B. MATHEWS

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NEW LEPIDOSTROBI FROM CENTRAL UNITED STATES

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 514

G. B. MATHEWS

(WITH SEVEN FIGURES)

Introduction

Knowledge of the structure of *Lepidostrobus* is based mainly on material discovered in Europe. The incrustations, of which many were described from the United States, furnish information concerning the external appearance of the organ or plant. Only three or four American species are recorded which were petrified and possible for anatomical study.

COULTER and LAND first described an American *Lepidostrobus* in 1911 (4, 5). The cones were found in Pottsville strata, near Indianola, Warren County, Iowa. In 1921 these investigators reported other cones from the same locality, but they could not expand the earlier description since the structure of the axis was not preserved in all the material. These specimens are now mainly in the collection of the Department of Botany at the University of Chicago, and are numbered: G21, P1-P11, and 502 (BF1, 21). JONGMANS (8, 9) named the cone described by COULTER and LAND *L. coulteri*. This *Lepidostrobus* is considered homosporous. In 1914 another species, *L. fischeri*, was described in detail by SCOTT and JEFFREY (13) from the Mississippian. It was later named *L. kentuckiensis* (14), since it was found in Kentucky, but the name which had been given it was preoccupied. In 1935 GRAHAM (6) described two kinds of small lepidostroboid cones from the Upper Connemaugh. These were found in coal balls from the Calhoun coal mine, Richland County, Illinois. Although these species are distinct from others hitherto described, the poor preservation of details led GRAHAM to leave the species unnamed.

It seems apparent that the cones upon which this study was made are of the same species as those described by COULTER and LAND (4, 5). The macroscopic features correspond well; the microscopic structures are the same, although COULTER and LAND could not give a description of the axis because it was not preserved. The cone with the best preservation is a cotype, G21 M1-M5. Another cone of which there are two sections in the collection is numbered G21 N1 and N2, and of the type specimen as described by COULTER and LAND (4) several slides have been made, G21 P1-P11. The variations in size of leaf traces as found in G21 M and G21 N and the differences in the structure of the lamina seem to be within the range of the same species.



***Lepidostrobus coulteri* Jongmans**

DIAGNOSIS

Cone large, 5–6 cm. in diameter; length up to 22 cm.

Axis 8–9 mm. in diameter.

Stele with central undifferentiated tissue; xylem 400–500 μ in thickness.

Leaf traces collateral; in outer portion of middle cortex 400–600 μ in diameter.

Ligule present; heel about 3 mm. long.

Parichnos present; bifurcates and branches, entering lamina.

Cortical layers about 3000–3400 μ thick.

Sporangium basal; palisade cells enlarged at corners.

Spores usually in tetrads of 52 μ , single spores 27 μ .

Lamina 12 mm. at base, $\pm$ ridged, 24 mm. long.

Geological horizon: Pottsville.

The following description is based on five sections in the collection of the Department of Botany, University of Chicago, G 21, M1–M5. This previously undescribed specimen was found years ago with other cones in a coal pocket near Indianola, Iowa, the same locality from which the specimen described by COULTER and LAND came. The geological horizon is Pottsville.

This specimen represents only a portion of the entire cone. The five thin sections show the anatomical features fairly well. A radial section through the upper portion shows the stem axis with stele and cortex and the arrangement of the sporophylls (fig. 1A). Only a few remnants of the laminae can be seen. Of the other sections, one is median longitudinal (fig. 1C), showing arrangement and position of structures in and outside the stele. From it the spiral arrangement of the sporophylls, shape of the heel and lamina, and many microscopic structures can be seen. The other longitudinal sections are more or less parallel to the median one. One section is slightly oblique, passing from the outer cortex at the lower part through the middle cortex and almost into the inner cortex at the upper part. A section parallel to this last shows sporophylls, pedicels, and sporangia in oblique view at the upper part and the leaf traces in the outer cortex at the lower part. Another tangential section is through sporophylls which are at right and oblique angles.

The following data about the size of this cone are based on these sections, since no record was available as to the actual size of the entire cone. The longitudinal sections are at most 51 mm. long; with the upper end, which had been cut off, the entire fragment was about 7 cm. long. One side of the cone is not preserved, thus the diameter can be estimated only from the known radius, which is 4 cm. The diameter of the axis tapers from 9 to 8 mm., which suggests a rather large cone, probably not less than 20 cm. in length. The shape is cylindrical. Calcium car-

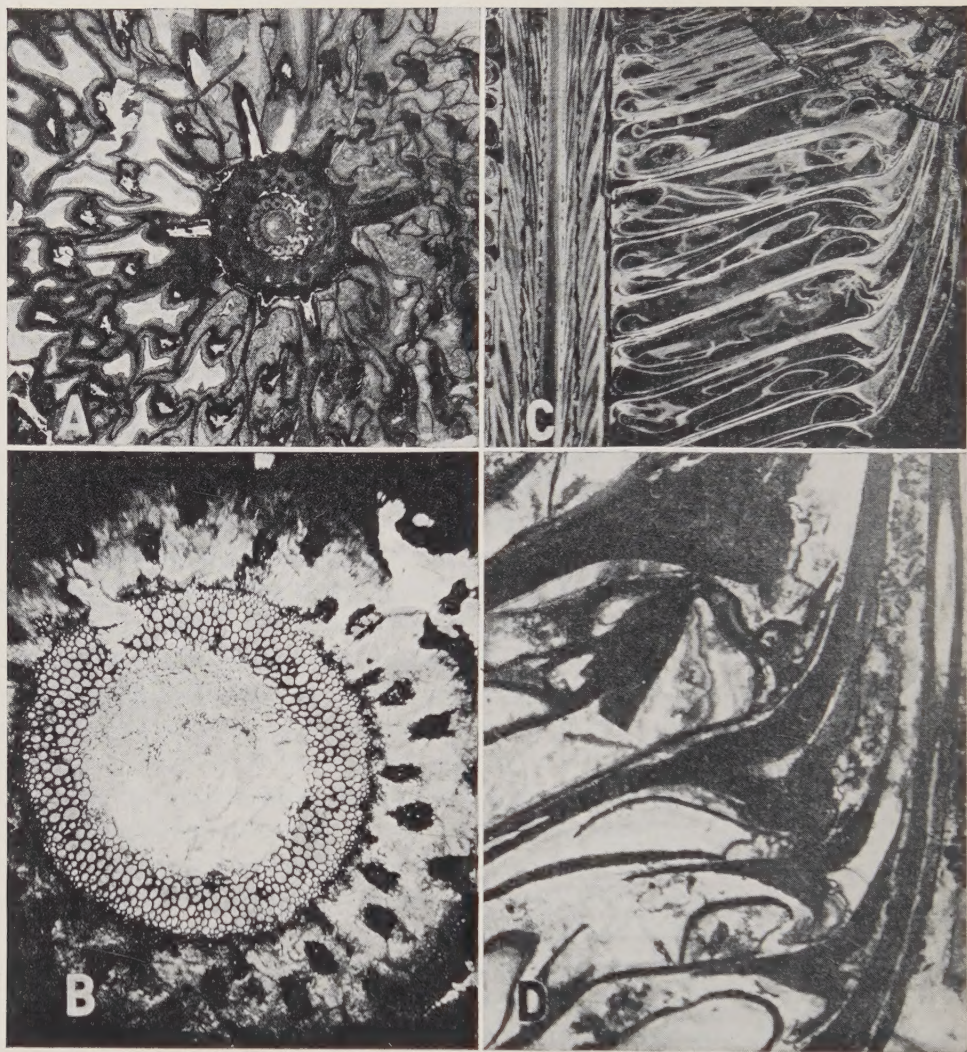


FIG. 1.—*A*: cross section of *Lepidostrobus coulteri* showing axis and sporophylls; G21 M5. *B*: part of *A*. Central portion of axis showing stele with protoxylem and metaxylem, central tissue in upper part, and empty space between stele and inner cortex. *C*: longitudinal section showing axis with tissues and arrangement and structure of sporophylls; G21 M1. *D*: part of *C* enlarged to show heel, parichnos, and leaf trace in lamina.

bonate was the main fossilizing agent. Other minerals, such as pyrites, were not noticed.

The lower and upper portions of the cone can be distinguished on the basis of several criteria: direction of the leaf traces in the axis, arrangement of the sporangia, relation between the pedicel and sporangium, location of the heel on the abaxial side of the pedicel, upward direction of the laminae, and other microscopic features. The spores were shed before fossilization, but here and there some are found in many sporangia. These spores are all of the same kind and apparently *in situ*.

CONE AXIS

The cone axis is cylindrical and has a diameter of 9 mm. at the lower end. It tapers a little to 8 mm. at the upper end in the distance of 51 mm. The radial and longitudinal sections show poor preservation of the central tissue, good preservation of metaxylem and protoxylem and of the inner and outer cortex, and fairly good preservation of the leaf traces in the stem axis. The core of the stele is not preserved except for some elements which are in contact with the metaxylem. These latter elements are of the same size as the mature metaxylem elements, 50–150 μ in diameter. All these cells have distorted cell walls, and of those most centrally located only the corners of the cells are preserved. The differences between these centrally located cells or “primitive fibers” and the metaxylem are that the former have little secondary wall thickenings and the end walls are at right angles to the longitudinal axis. While there are these slight differences, many similarities lead to the conclusion that these cells are to be regarded as undifferentiated metaxylem cells.

Adjacent to these central cells are the larger elements of the metaxylem. They have a diameter of 30–120 μ , while the thickness of the whole belt is 400–500 μ . The long section shows that there were eleven scalariform thickenings per 100 μ of length in the central part and that the number of thickenings increases peripherally to fourteen and twenty-two per 100 μ . The metaxylem elements gradually merge into the smaller elements of the protoxylem strand. The spiral thickenings of these latter are closer together, about thirty-six per 100 μ . The gradual transition is shown also by the decreasing diameter of the metaxylem elements and transitional forms of the thickenings. No longitudinal striae between the thickenings were noticed.

The cylinder of tissue just peripheral to the xylem is not well preserved. It is about 300–400 μ in thickness. A few remnants are present here and there, of small diameter (12–30 μ) and parenchymatous. The space occupied by this layer is the one in which the endodermis and the pericycle might be differentiated, but these structures could not be clearly discerned. The leaf traces are preserved in this belt.

The cortex, which is differentiated into an inner, middle, and outer portion, thus resembles many forms already described. The inner cortex is bounded centrally by the inner space just mentioned. The crenulated outlines of the inner cortex are associated with the leaf traces, which extend through this tissue. A tangential gap occurs (fig. 1B), the total width therefore varying from 600 to 1000 μ . The polygonal cells are of various diameter, from 30 to 75 μ , with a length of 110 μ . From the longitudinal sections it is apparent that the cells of the inner cortex are not parallel to the strands in the stele in their longitudinal axes. The cells (or better, the cell walls of the inner cortex) gradually merge into the empty space peripheral to the inner cortex. The middle cortex, which was present where the space now occurs, is rather thick, almost 2 mm. No trace of any structure of the tissue formerly occupying this space could be detected. As in other forms, perhaps this trabecular tissue was too delicate to withstand the decaying influences before fossilization took place. From the rootlets and other structures of foreign origin present in the specimen, it is clear that fossilization took place a considerable time after the cone was detached from the tree. The parichnos, however, which extends from the middle cortex, may reveal something about the cellular peculiarities of this part of the cortex.

The leaf traces are well preserved as they extend through the middle cortex. The outermost portion of the stem axis is the outer cortex, a rather dark sclerenchymatous tissue 400–800 μ in thickness. Two kinds of cells can be distinguished. The inner ones are tangentially elongated and radially flattened, 25–30 $\mu \times$ 12–15 μ . Several layers farther out the cells are isodiametric and spherical. In general the outer portion of this tissue is rather dark, and few details can be discerned. The lumen of these cells is 12–10 μ . This layer abuts the bases of the sporophylls, the pedicel.

The sporophyll is composed of the pedicel and the sporangium (fig. 1C). The maximal length for the pedicel up to the heel is 22 mm. The pedicel and with it the sporangium has a slightly upward direction, but the angle is not the same at both sides of the axis, owing to unilateral pressure. The pedicel is of triangular shape where it leaves the axis. For a short distance it is not connected with the sporangium, since no attachment of the sporangial tissue can be noticed and the epidermal layer is continuous around the pedicel. As the pedicel continues on the way out, it flattens and enlarges on both sides. Almost at the point where the sporangium ends, a strong downwardly projecting heel 2.5 mm. long is developed. The pedicel continues in a straight upward direction as lamina. The shape and size of the lamina are perceptible from several sections. The length is 24 mm., with a maximal width at the base of its origin of 12 mm. From the fact that each lamina shows a markedly enlarged portion on its section it is concluded that it had an abaxial ridge in which the vascular bundle was located. The blade of the lamina

is in some places $150\ \mu$ thick, while the vein has a thickness of $400\ \mu$. The thickest lamina was about $800\ \mu$ at a distance 8 mm. from the heel base. The pedicel thus enlarged from 1.3 mm. at the very beginning and 3 mm. at the base of the heel to a lamina 12 mm. in width and a total length of 46 mm.

PEDICEL

The heavy sclerized cortex is continuous with the pedicel. The sclerotic tissue surrounds the vascular bundle and the parichnos on all sides except in the region of attachment of the sporangium. In this latter area the adaxial epidermal and hypodermal layer is replaced by another tissue for almost the entire length of the sporangium. The tangential width of this connective tissue varies with the size of the pedicel at that special point. Usually it is in a relation of 2:5. From this tissue arise the sporangial wall, the tapetal tissue, and the subarchesporial pad. The heel has a peculiar structure. On the abaxial side no strong epidermal layer is present. The subepidermal layers have been destroyed up to $400\ \mu$ into the tissue, and the empty space shows that this tissue was probably of delicate nature, although the epidermal layers show a wavelike contour over the heel. They assume the usual strong habit of dark epidermal and subepidermal tissue after 3–5 mm. The heel is filled with parenchymatous cells. The cells below the parichnos are of various size and extend at a right angle to the leaf trace but are arranged parallel to one another. The tissue which separates the leaf trace and the parichnos is more regularly arranged in vertical and horizontal rows several layers in thickness. The trapezoidal cells are $50\text{--}80\ \mu$ long with a median diameter of $25\ \mu$. On the adaxial side of the heel the hypodermal layer is built up of rather long sclerenchymatous cells, $300\text{--}400\ \mu$ long and $20\ \mu$ broad. In the lamina the cells are isodiametric, especially those near the parichnos, and resemble cells of mesophyllous character. Small intercellular spaces are interposed among the cells adjacent to the parichnos.

SPORANGIUM

The sporangium is attached to the adaxial side of the pedicel and is 22 mm. long, 4 mm. high, and 5 mm. broad. The sporangia are mostly empty, although in many of them a few spores remained in the distal and proximal parts. By the flap at those parts pouches are formed which probably inhibited the spores from escaping. These spores are found in almost all parts of the cone, in the lower as well as in the upper section. The sporangia were ripe when fossilization took place, and the sporangia open, but some structures permit certain conclusions about the shape of the mature sporangium. On each lateral sporangial wall are two points where the cell walls are larger and functioned apparently for the stiffening of the wall. These enlarged palisade cells appear distinctly at almost the same loci in the cross-sectioned walls. They indicate the corners of the sporangial bag. The first thickening

is near the base at a distance which corresponds to the length of the wing of the pedicel. The next is about 1 mm. or more in front. After this follows the last portion, which is always a little longer than half the width of the relative pedicel at that point. Thus the mature sporangium would be of the usual shape, with a thickening on the four corners. The palisade cells are in general $75\ \mu$ high. At the corners they reach $125\ \mu$ but decrease toward the point of dehiscence to $25\ \mu$, while the diameter remains $16\ \mu$. The inside of the sporangium is lined with the tapetal layer, which is gone except in some instances at the distal or proximal pouches. These thin-walled elongated cells line the sporangium wall, sometimes eleven cells deep, to a total thickness of $140\ \mu$. The subarchesporial pad is composed of extremely delicate cells. No definite arrangement of sterile tissue plates was noticed.

SPORES

All except a few spores were shed. They are mainly single but in some instances are arranged in tetrads. Their surface is simple. The diameter of a tetrad is $52\ \mu$, while the largest diameter of a single spore is $27\ \mu$. The fact that they are of the same size and shape at the lower as at the upper part of the cone fragment leads to the conclusion that the cone was a staminate one or the plant homosporous.

LEAF TRACES

The arrangement of the leaf traces in the axis and sporophyll is visible in the long and cross sections (fig. 1A, B, C). The bundles take their origin from the points of the peripheral protoxylem. At the point of departure from the vascular cylinder there are about nine elements present, not surrounded by any preserved tissue. As the bundles go farther away from the stele, a surrounding sheath develops. These cells have a brownish appearance, while the xylem cells have a whitish crystalline content. The cells which compose the sheath are longitudinally elongated, with walls at right angles. The shape of the leaf trace in the inner space is radially elongated in cross section but becomes cylindrical as it gains distance from the stele. The number of xylem elements increases to about twenty-three but is not constant. The smaller protoxylem elements are usually in a mesarch position and number about seven.

With the approach of the leaf trace to the inner cortex, the appearance of a phloem portion in the trace becomes apparent. Where the leaf trace nears the inner cortex the tissue of the latter recedes, bulging away from the trace. At the same time the tissue which surrounds the trace sends out two lateral peripheral projections. These unite with the inner cortex, leaving between them an empty space which probably had been occupied by the phloem. A phloem strand in connection with the leaf trace cannot be seen in the inner space, probably because this belt was filled with parenchyma, which was not preserved. The vascular bundle

shows a different structure in its passage through the inner cortex. An empty space accompanies the leaf trace on its abaxial side. A sheath surrounds the bundle as a whole and the xylem strand which is separated from the phloem by the conjunctive tissue.

The delicate phloem tissue is not preserved at any place in this fragment—except for a small portion which probably had been broken off before fossilization began and thus had a chance to undergo mineralization by quick infiltration before decay started. The space occupied by the phloem in the inner cortex is cylindrical. Its tangential diameter decreases peripherally, while the radial one increases. Conjunctive tissue separates the xylem from the phloem. A different sheath surrounds the whole bundle as it passes through the middle cortex. This sheath is of the same structure as the tissue of the inner cortex. On the whole, except for size, the leaf trace in the middle cortex has the same arrangement and structure as in the inner cortex. In the middle cortex only the leaf trace is preserved, without a trace of the surrounding tissue. As in entering the inner cortex, the tissue of the outer cortex bulges back where the leaf trace approaches, but no projections of the sheath are formed. The clear phloem space in the bundle becomes flattened radially until it is crescent-shaped. A few remnants of cell walls on the periphery of the empty space indicate cells of small caliber. Another empty space appears in the outer cortex. It lies abaxial to the bundle as a continuation of the tissue of the middle cortex. In the same way that the phloem became apparent only in the next belt, the inner cortex, and the cortical bundle sheath in the middle cortex, so the parichnos shows up in the outer cortex, which is the following tissue. The soft delicate tissue is not preserved. The tangential width of the parichnos is the same as that of the whole bundle. The radial diameter is almost the same as that of the phloem. The total length of a leaf trace in the stem axis from the point where it leaves the protoxylem ring until it enters the pedicel varies from 1.5 to 2.5 cm.

These data are not taken from a single bundle, since none is cut longitudinally its whole length; they are based upon measurements of various leaf traces in different tissues of the cylinder. The course of the leaf trace is shown in the longitudinal axis. All leaf traces are cut in the same plane. On the upper end the traces are just leaving the inner cortex. A rather large portion is cut, about 3 mm. It runs parallel to the plane of cutting, while in the outer cortex the cut leaf trace measures almost 1 mm. in length, although enlarged during the journey through the cortical layers. The explanation is that the course of the leaf trace is rather steep in the beginning but becomes more horizontal in the outer half of the outer cortex. In the pedicel the position of the leaf trace is on the adaxial side close to the sporangium. Surrounding the leaf trace in the heel are the barred cells of the transfusion tissue on the adaxial side. These cells run not only parallel to the leaf trace but also at right angles to it. They accompany the leaf trace into the lamina and

are located laterally to it. There is no space left on the ventral or dorsal side because the trace fills out the space completely. An abaxial keel is formed which is rather prominent in comparison with the thin blade of the lateral wings of the lamina. At a distance of 22 mm. from the heel base, a leaf trace was noticed about $300\ \mu$ thick. There three xylem strands could be seen surrounded by a mass of thin-walled elongated cells with oblique walls.

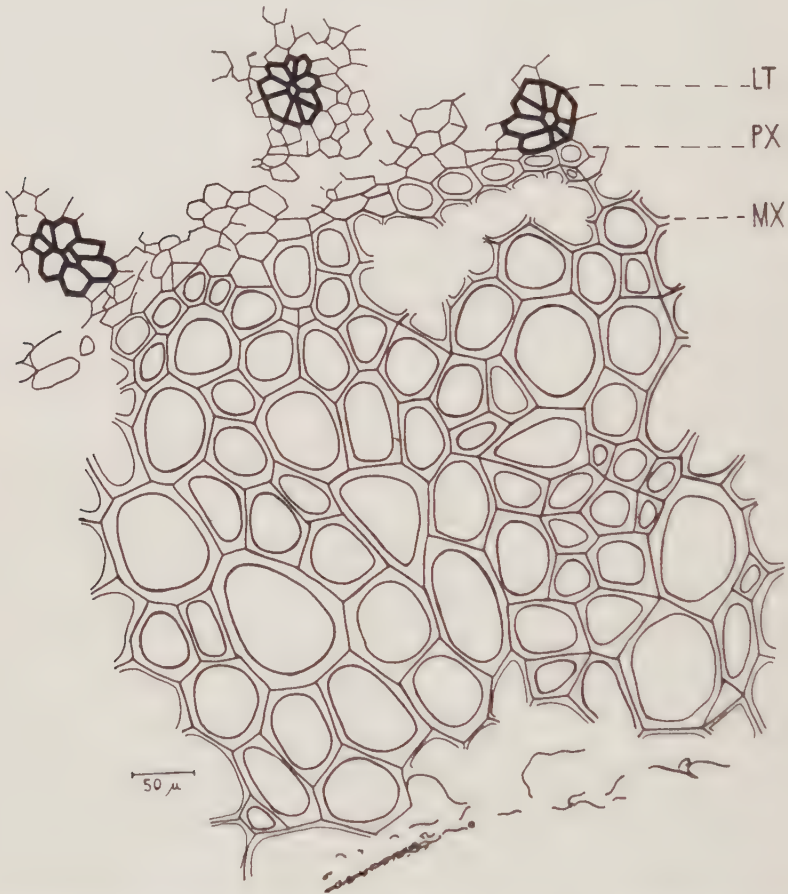


FIG. 2. Axis of *Lepidostrobus coulteri* showing decayed central tissue, metaxylem, and protoxylem (*mx*, *px*), and some leaf traces (*lt*); G21 N1.

PARICHNOS

The parichnos extends from the middle cortex and is first noticed in the outer cortex on the phloem side of the leaf trace. It connects the lacunar tissue of the middle cortex with the intercellular spaces of the lamina. At about two-thirds the

length of the pedicel the parichnos splits off into three branches. The median one is at first bigger but soon decreases and after a short distance fades out, while the two lateral ones continue. In the heel the parichnos has a radial or tangential diameter of $300\text{--}500\ \mu$ but decreases rather rapidly in width (fig. 1D). In the lamina it is surrounded by cells with intercellular spaces, two layers on the abaxial and one on the adaxial side. The space taken by the parichnos corresponds almost to the width of one cell layer of the surrounding tissue— $30\ \mu$.

Two other mounted sections were found in the collection, G21 N1 and N2. One is a complete radial section; the other shows about a quarter of a radial section with the entire axis. These sections are (*vide* Dr. A. C. Noé) from the same locality as the first cone described. Both sections are no doubt from the same specimen. The external appearance suggests the same composition as that of G21 P, but in this specimen pyrite crystals fill the cells here and there.

The diameter of the cone is 6 cm., laminae included. The axis measures 8 mm.; the distance between the axis and the lamina is 2 cm. The central tissue is not preserved except for a few remnants. These are compressed and show as a rather sharp line separating the empty central space 1.3 mm. from the xylem, which is $500\text{--}600\ \mu$ in thickness (fig. 2). The next zone is not preserved except for a few cells bordering on the protoxylem, and the leaf traces.

An approximate estimate can be given for the thickness of the space between xylem and inner cortex. From the preceding description it is evident that lateral projections extend peripherally from the leaf traces as they approach the inner cortex. The projections are preserved, the tissue of inner and middle cortex being destroyed. The space between xylem and inner cortex is about $600\ \mu$ thick. The following space, occupied formerly by inner and middle cortex, measures $2100\text{--}2400\ \mu$. The leaf traces near the outer cortex measure $400 \times 500\ \mu$, with a phloem space of $175 \times 75\ \mu$. They are smaller than those of the previous cone, with $600 \times 600\ \mu$ and a phloem space of $200 \times 150\ \mu$. The laminae are known only in cross section. The width of the lamina in the first peripheral row is 12 mm. Farther out in the third row some are $1800 \times 500\ \mu$ and $700 \times 300\ \mu$. The middle vein is not sharp. The few spores measure $25\ \mu$. They are shrunken and attached to the sporangial wall.

***Lepidostrobos noei* sp. nov. Mathews**

DIAGNOSIS

Lepidostrobos noei Mathews, centimeter 15 longus, 7 crassus, bracteis millimeter 8–20 longis, laminis medio-costatis millimeter 14 longis, 8 latis; sporis dimorphis magnitudine comparatis ratione 1:5, microsporidis minutis quaternatim conjunctis millimeter 0.050; macrosporidis millimeter 0.275–0.330 innumerabilibus sporangia inferioris tenentibus.

Cone large, heterosporous, 7 cm. in diameter and more than 15 cm. long (actual length of fragment 11 cm.).

Axis without central tissue, 7 mm.

Stele with central tissue of undifferentiated xylem; xylem layer 300-400 μ thick.

Phloem surrounding the xylem.

Pericyclic fibers present.

Leaf trace collateral; xylem elements more than thirty; diameter of leaf trace (with slight variation) 100 μ in axis.

Parichnos not extending into peripheral part of outer cortex.

Sporangia basal, five-sided polygon, sterile plates short, unbranched.

No heel present.

Megaspores numerous in sporangia at base of cones, smooth, with triradiate ridge, 275-330 μ .

Microspores in sporangia at top of cone, tetrads 76 μ , single 50 μ .

Laminae 8 mm. broad, with sharp vein; 14 mm. long.

Geological horizon: Upper Devonian (?).

The new cone is named after the late Dr. A. C. NOÉ.

This cone was found near Gartersville, Garrard County, Kentucky. It was forwarded to Dr. A. C. McFARLAN of the Department of Geology at the University of Kentucky, Lexington. Dr. A. C. NOÉ, University of Chicago, to whom the cone was sent for classification, gave it to the writer for a superficial study. When it was found that the cone was heterosporous, all efforts were made by Dr. NOÉ to get permission from the respective authorities in Lexington to section the cone and make a detailed study. The sections and slides are now in the Department of Botany at the University of Chicago, nos. G22 M1 M33. A big fragment showing a long section and partial radial section with the external structure intact is now in the Department of Geology, University of Kentucky, no. M3121. As to the geological horizon, Dr. McFARLAN wrote that the cone was found "on the edge of the Knobs, which would make possible its occurrence in either Ohio or New Providence shales. It is unfortunate that the precise horizon is not known." The Ohio shale would place the cone in the Upper Devonian; the New Providence shale, in the Mississippian. The New Providence shales contain only marine fossils, as is known until now. Before any sections were made, some excellent molds were made in plaster of paris by the courtesy of the Daprato Statuary Company, Chicago, Illinois.

GENERAL DESCRIPTION OF CONE

The cone is a petrified specimen and is almost free from adherent foreign material, so that the external structure can be seen. The color on the outside is gray and inside, brownish. At the lower part a greenish taint was caused by the pres-

ence of algae and protonemata of mosses. The fructification was exposed to climatic influences for considerable time. On the lower part a few sporophylls were broken off. On one side the laminae are not present for almost the entire length of the cone. Fossilization of the cone is no doubt excellent; the mineral, however, is mainly calcium carbonate and is decayed to a large extent. Peels do not therefore reveal the details. The observations and pictures were made mostly with reflected light. Some of the megaspores were replaced by siliceous compounds, others by pyrites. The connective tissue between pedicel and sporangium is not preserved but is replaced by transparent calcites.

The length of the fragment is 11 cm. (fig. 3*B*). The maximal width is 7 cm., about 8 cm. from the lower end. The cone is wider at the middle, tapering toward the top and bottom. By pressure of unknown forces the cone—and with it the axis—was deformed from a cylindrical to an elliptical shape, so that the diameter varies. The small diameter is 5.5 cm.; the large one is 7 cm. Compression occurred in such manner that on one side the laminae were appressed and the cone broke longitudinally. The halves were disarranged, so that on the same radial section the cone axis on one side measures 2.5 cm. in thickness (except the central tissue) and on the other side 3.1 cm. The weaker central tissue is mostly crushed. All laminae have been broken just at the point where one would look for the ligule. Where the laminae had been broken off before fossilization, decaying processes have exposed spores and the structure of the pedicels. The spores could be seen with the naked eye and filled the sporangia in great masses; surely megaspores. A small piece of a broken sporangium from the upper end contained spores much smaller than the megaspores in the sporangia below. In the same uppermost whorl were also some megasporangia; thus this whorl consisted of mega- and microsporophylls.

An upper part, 1.8 cm. in thickness, was cut off radially to study the arrangement of mega- and microsporophylls, which seemed to be unusual. The remaining lower portion was sectioned tangentially near the axis. Another radial section was then made, since the structure of the axis was found not to be well preserved in the uppermost portion. Other sections were cut parallel to the longitudinal sections at 4 mm. intervals. In these sections the details of all organs were exposed.

The general arrangement of the parts in this cone is very similar to that described from other strobili of this genus. The stele is surrounded by a well-preserved parenchymatous layer. The cortex is composed of three layers, exceptionally well-preserved tissues. The outer cortex is continuous with that of the pedicel. The sporangium is attached to the adaxial side of the pedicel for almost its entire length. The pedicel does not develop a heel but bends up, becoming the lamina which overlaps several sporophylls (fig. 3*A*). The megasporophylls are found in the lower part of the cone and the microsporophylls in the upper part. The axis tapers gradually toward the upper end, but the shape of the cone does not corre-

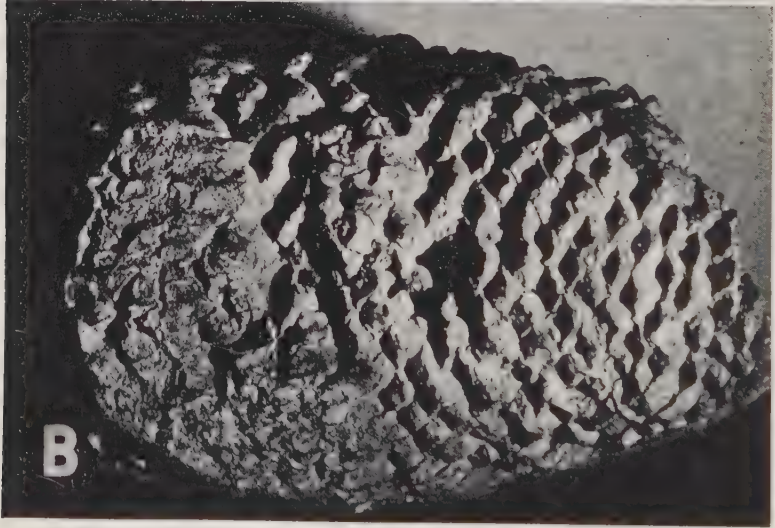


FIG. 3.—*A*: longitudinal tangential section of *Lepidostrobus noei* showing arrangement of megasporophylls and laminae; M₃₁₂₁. *B*: external view.

spond to this feature of the axis. From the axis the conclusion may be drawn that the cone was about 15 cm. long. Thus in the lower two-thirds are megasporophylls with microsporophylls in the upper third.

CONE AXIS

The central portion of the stele consists of cells which are considered to be undifferentiated xylem elements. Not all are preserved. Those preserved show that they are of the same size and shape—except for the thinner walls and lack of secondary thickenings—as the adjacent metaxylem elements. Owing to the crushing of these cells their exact shape can be determined only by comparison with metaxylem elements. The central cells have no content, are rather long, and their cross-walls are pointed or at right angles to the longitudinal axis. The name pith cannot be applied to this tissue. The xylem is continuous with the central tissue and has a centripetal development, with the protoxylem elements on the outer periphery.

The following measurements are given from the side of the shorter diameter. The metaxylem belt is eight to twelve cells deep, with a total thickness of 300–400 μ . The elements vary from 50 to 130 μ in diameter and have scalariform thickenings. The larger elements are filled with a centrally located substance an average distance of 12 μ from the wall. Elements of less than 25 μ therefore do not have this infiltration. The middle lamella of the cell walls shows up clearly as a black line between the light brown walls. The structure of the stele is exarch, the protoxylem elements being located at the periphery of the stele. These protoxylem elements are smaller, about 20 μ in diameter. The abaxial circumference of the xylem belt is regularly pointed by protuberances of the protoxylem. These are the beginning points of the leaf traces. The protoxylem abuts on a cylinder of parenchymatous cells. It is this layer which in most of the cones described is poorly or not at all preserved. In this cone, however, the preservation is excellent. A camera lucida drawing was made of an area of this parenchymatous region to show all possible details (fig. 4).

The protoxylem is bordered by a zone of two to six tangentially elongated cells measuring about 25 μ in length and 8 μ in width. The walls are thin, the black corners show up sharply, and no intercellular spaces are seen. This zone is interrupted where a leaf trace is to be given off and is several layers in thickness where a leaf trace is to emerge. It resembles the phloem of the leaf traces and represents, by its position and anatomical character, tissue which can be called phloem. Just peripheral to this cylinder is another belt of parenchymatous tissue containing numerous leaf traces. These two parenchymatous cylinders are not clearly delimited from each other. The outer limit of the peripheral layer can be identified by a peculiar layer of cells. They are thin-walled, elongated tangentially, and their radial walls are here and there crushed and zigzag in shape. In connection with the

cells in the pericycle are found one or more cells with thick walls representing pericyclic fibers (fig. 4*pf*). The innermost layer of the cortex consists of cells of larger diameter ($40-70\ \mu$) with a central heterogeneous filling. These cells abut peripherally on a trabecular tissue, which is well preserved. This belt measures $400-800\ \mu$ in diameter. The elongated cells range in length from 30 to $200\ \mu$, and run in various directions. The cells on the inner border of this belt usually begin with a smaller diameter than that of the adjacent cells, but enlarge from 6 to $30\ \mu$. Even in the same cell the diameter varies, giving this tissue an irregular appearance.

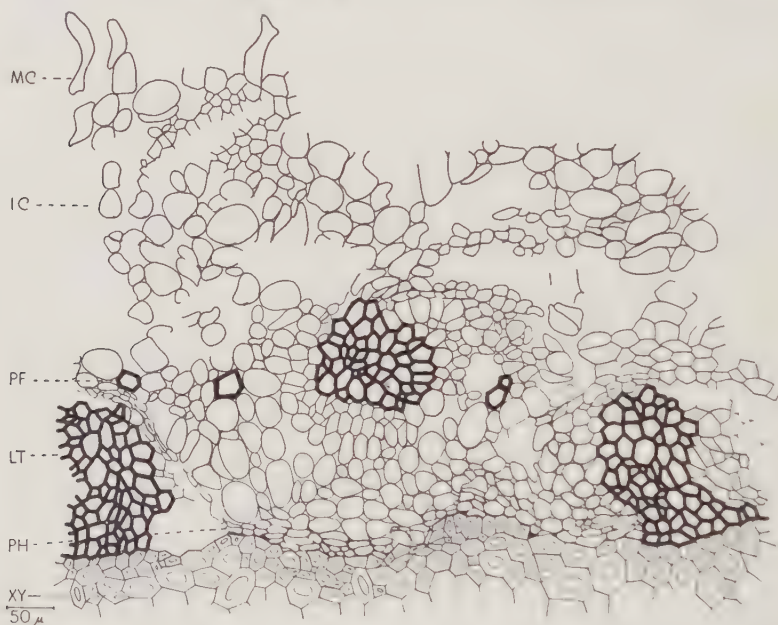


FIG. 4.—Part of axis of *Lepidostrobis noei* (xy, xylem; ph, phloem; lt, leaf trace; pf, pericyclic fibers; ic, inner cortex; mc, middle cortex).

The aerenchymatous nature of this tissue is apparent. The outer cortex starts abruptly and is $1100-1200\ \mu$ in thickness. It is made up of two kinds of cells, in two concentric layers. The cells of the inner ring gradually merge into the outer tangential belt. In some instances an irregular black line separates these layers. Among the outer cortex cells of the inner portion intercellular spaces are interspersed, and the diameter of the cells varies a little. On the whole they have a homogeneous content. Although a sharp line cannot be drawn between the peripheral and the central portion, a difference is indicated by the different structure and arrangement of the cells. The cells of the outer portion are arranged in more or less clear radial rows and the diameter decreases peripherally to $23\ \mu$, especially where a pedicel is to leave the axis.

SPOROPHYLLS

The sporophylls branch off from the axis at almost right angles, but the inclination of the sporophylls with the axis varies. In the lower portion it is at 70° ; at the upper part, at 80° . The sporophylls are arranged in spirals. The phyllotaxy is 2:51. Some indication of this arrangement may be noticed in the regular appearance of the lamina and sporophylls in the long section (fig. 3A). The sporophyll is composed of the basal pedicel and the upper sporangium. The pedicel is continuous with the outer cortical tissue of the axis and has cells of the same sclerenchymatous structure. The connective tissue between pedicel and sporangium is in no case preserved, but from the absence of the sporangial wall on the abaxial side of the sporangium it is apparent that the latter was attached to the pedicel for almost its entire length—except for a small distance on the proximal and distal ends. The fragment of the cone represents the lower portion. The lowermost sporophyll is 7 mm. in length, the uppermost 22 mm. When at first the pedicel becomes free from the axis it is triangular in cross section and 2 mm. in the longest diameter. The horizontal diameter is always smaller than the overlapping sporangium, except at the distal end. Here the pedicel enlarges laterally to 5 mm. As the sporangium tapers at the periphery of the cone the pedicel enlarges and becomes rounded on its abaxial side. The cells of the pedicel are of the same structure as those of the outer cortex, isodiametric, sclerenchymatous. The leaf trace runs on the adaxial side. The epidermal cells have thick walls and are arranged in one layer. No difference was noticed between pedicels of mega- and microsporophylls.

SPORANGIUM

The sporangium is attached to the adaxial side of the pedicel. Both mega- and microsporangia are found in *L. noei*. The structure is the same, except the spores. The shape of a sporangium in cross section is shown in figs. 3A, 5B. It measures 2×2.2 mm. By this shape all sporophylls match perfectly. The sporangium is slightly larger than the pedicel, except at the distal end, where the sporangium flattens and tapers tangentially. The connective tissue forms a rather narrow band and is about one-fifth the total width of the pedicel. The walls of both the mega- and microsporangia are made up of typical palisade cells, $25 \times 25 \mu$ in size. No difference was noticed in the size of these cells at the corners or on the tip of the sporangia. Inside these wall cells is another layer of jacket tissue made up of elongated cells in which a dark spot (nucleus?) can be seen. In the palisade cells a dark spot is located at the outer periphery (fig. 5D). The tapetum centers the jacket cells. It is conspicuous all round the sporangium but is especially well developed at the corners, with a depth of eight to eleven cells. These cells are continuous with the subarchesporial pad. All sporangia are in the mature stage and not yet opened. About the mechanism of dehiscence no peculiar structure could

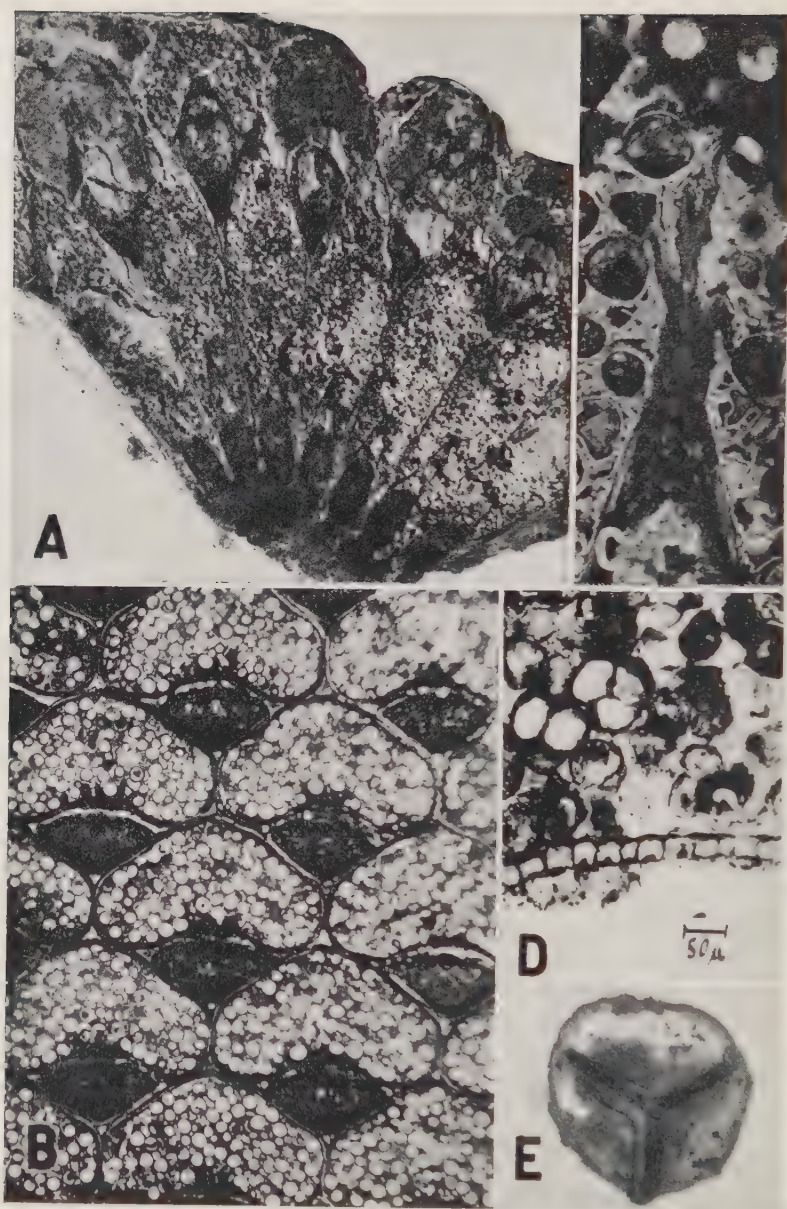
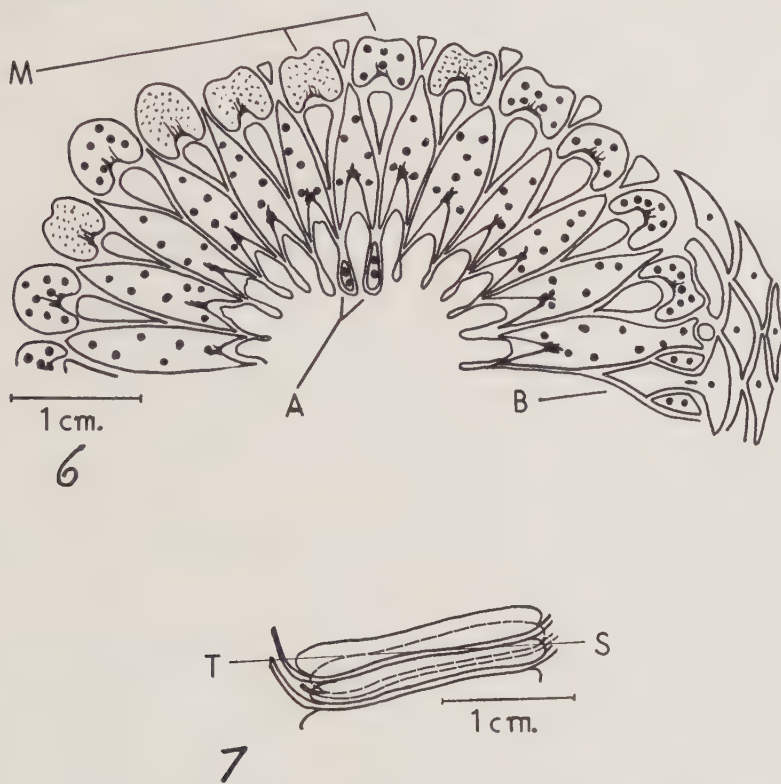


FIG. 5. *Lepidostrabus noei*. A: cross section of cone showing arrangement of micro- and megasporophylls; B: tangential section showing megasporophylls; C: oblique section through megasporophyll showing sterile tissue plate and megaspores; D: microsporangium with microspores in tetrads and sporangial wall; E: megaspore.

be noticed in the wall. Sterile plates arise from the subarchesporial pad in both the mega- and microsporangia (fig. 5C). In more oblique sections these plates are finger-like projections.

ARRANGEMENT OF SPOROPHYLLS

The arrangement of the mega- and microsporophylls is peculiar. Figure 6 represents a drawing from a photograph of a radial section through the upper part of



FIGS. 6, 7.—*Lepidostrobus noei*. Fig. 6, arrangement of micro- and megasporophylls. Fig. 7, diagram showing plane of section as given in fig. 6.

the cone. It shows in the peripheral layer thirteen sporophylls—eight megasporophylls and five microsporophylls. The microsporophylls originate separately at three different loci in the same spiral. The median circle represents only megasporangia; the inner circle shows in two instances megasporangia (fig. 6A). It would seem that these sporangia are the same as are cut again at the outer circle, which would mean that the same sporangium (A and M) has megaspores and microspores. From a longitudinal section, however, the solution of this striking feature can be explained in another way. As shown in figure 7, three whorls are

cut longitudinally, of which the upper and lower sporophylls are on the same orthostichy; the median is interlocking. If the upper sporophyll is a microsporophyll and the lower ones are megasporophylls, it is apparent that by a radial section (as indicated by the line *T-S*) the arrangement of sporophylls will be a microsporophyll at the outer circle and a megasporophyll at the median and inner circle. Figure 6 shows various stages of the relation between pedicel and sporophyll. At various points the sporangium overlaps the pedicel, and at *B* the sporophyll is cut in such a way that the pedicel is seen to be continuous with the lamina, while small lateral portions of the overlapping sporangium have been cut off. The pedicels have the same structure in both kinds of sporophylls, although it seems (fig. 6) that the pedicels of the microsporangia are smaller than are those of the megasporangia.

SPORES

The megasporangia are filled with numerous megaspores. Some are wholly replaced by pyrites, siliceous compounds, or calcites. After maceration of some megaspores with HCl the thin spore wall remained, which made a detailed study of the spore wall possible. The megaspores measure $270-330\ \mu$ and show triradiate markings, each about $120\ \mu$ long. The megaspores are separate. Here and there crushed megaspores are seen. The microsporangia are in the upper part of the cone. From a reconstruction on the basis of the preserved axis apparently the upper third of the cone had microsporangia. The microspores are arranged in tetrads (fig. 5*D*). The diameter of a tetrad is $76\ \mu$; of a single spore, about $50\ \mu$ in the longer axis. In sections of the microspores often exosporium and endosporium can be seen.

LAMINA AND LIGULE

As previously mentioned, the laminae are broken at the point where one would look for the ligule (fig. 3*A*). It was not possible to locate with certainty a structure which might be considered a ligule. The lamina starts with a constriction of the pedicel. It is at that point cylindrical or triangular in cross section, with a diameter of $3.5-4\ \text{mm}$. Soon the lamina widens tangentially to $8\ \text{mm}$. On the surface of the cone where the laminae are preserved a small longitudinal median ridge can be seen on each lamina. The longest lamina was $14\ \text{mm}$.

LEAF TRACES

The leaf traces are well preserved. The starting points are protoxylem elements on the periphery of the stele (fig. 4). The number of such elements is about ten when the leaf trace is freed from the xylem belt. The trace is $100\ \mu$ in diameter. The smaller elements are in the center and probably represent the protoxylem. As the leaf trace passes into the parenchymatous layers, the cells adjacent to the bundle are arranged around it like a sheath. In this parenchymatous belt more leaf

traces can be seen than in the regions which follow peripherally. On the abaxial side of the leaf trace a few small, thin-walled cells are separated from the xylem by a layer of parenchymatous cells which represent the beginning of the phloem strand. The leaf trace does not enlarge much as it passes through the trabecular tissue of the middle cortex. In the outer cortex very few leaf traces are seen. Near the middle cortex these traces may be surrounded on all sides with trabecular tissue, although a layer five or more cells in thickness may separate the trace and the middle cortex. A parichnos strand was not noticed in the peripheral part of the cortex or the pedicel. At the entrance of the leaf trace into the pedicel the diameter of the trace is not increased. When the trace bends in the outer cortex to enter the pedicel, the arrangement of the cells outside the bundle on the phloem side is changed. The sclerenchymatous cells on the adaxial side run in their ordinary straight way and simply abut on the bundle sheath; the cell on the abaxial side bend to enter the pedicel. Just at this point parenchymatous cells parallel to the main axis are seen which connect the leaf trace with sclerenchymatous cells. This layer is about $300\ \mu$ in thickness. In the pedicel the leaf trace runs on the adaxial side, phloem downward. It is larger than in the axis and has a radial diameter of $200 \times 500\ \mu$, of which the latter means the axis in the xylem-phloem direction. In the lamina the leaf trace takes a central position, is of large diameter ($400 \times 500\ \mu$), and collateral. The epidermis is composed of a layer of thick-walled cells.

Discussion

A comparison of *Lepidostrobos coulteri* and *L. noei* with the already described species of *Lepidostrobos* does not reveal many striking peculiarities in these new cones, but they appear to be good distinct species.

In size the cones agree with *L. brownii* (17), which has a diameter of 5-7.5 cm., and with *L. kentuckiensis* (13) and *L. bertrandi* (16), which have diameters of 5 cm. Data of the actual length of the cones are not always available, for generally only fragments are known. The longest in this group is *L. coulteri*, with an actual length of 22 cm. (5).

The axis varies much in size and structure in this genus. The ratio between the diameter of cone and axis is not constant: in *L. brownii* (17) it has a range of from four to ten, in *L. coulteri* and *L. delagei* (17) about seven, in *L. oldhamius* (11) five to ten, in *L. noei* about ten, in *L. bertrandi* (16) four, in *L. kentuckiensis* (13) five, and in *L. binneyanus* (1) three. In *L. masleni* (3) the axis decreases from 1.28 mm. at the base of the cone to 0.53 mm. at the top. The diameter decreases in the same ratio. This is not true in *L. noei*.

According to the structure of the stele the cones may be placed into three groups. To the first group belong the protostelic forms with xylem throughout, such as *L. schimperi* (17). In a second group can be placed those forms which have

not developed a special pith tissue but have central undifferentiated embryonic tissue. Here belong the forms described as having "fibres primitives," as *L. brownii* (17), *L. kentuckiensis* (13), and *L. bertrandi* (16). In this group fit also *L. coulteri* and *L. noei*. To the third group belong the forms with a central pith—the siphonostelic cones, as *L. binneyanus* (1), *L. masleni* (3), and *L. arberi* (1). From the phylogenetic standpoint, considering only this character, the first group probably is the most primitive while the last one with a pith is most advanced. The forms in the second group bridge the other two groups.

In the central embryonic cells of *L. coulteri* and *L. noei* are found thin walls and walls with thin scalariform thickenings, pointed cells with oblique cross-walls, and cells with end walls at right angles. In all forms the scalariform elements are central, while spiral or annular thickenings are found in the peripheral protoxylem elements. The nature of the region just outside the xylem cylinder is much disputed. This is due not only to insufficient preservation in most forms, but partly to a real difference in the arrangement of tissues in different cones and partly to a lack of uniformity of nomenclature. The tissue surrounding the xylem belt was probably of delicate nature. If it did not decay it became crushed and only in a few cases is it well preserved. These small cells of a parenchymatous nature were called cambial cells in *Lepidodendron* by WEISS. SEWARD and CAMPOS (3) consider them meristematic. BERTRAND described them as "fibres primitives" and considered them related to phloem cells. MASLEN (11) speaks of them simply as parenchymatous cells. BOWER (2) did not recognize any phloem, although the specimen he described was well preserved. SCOTT (15) calls them phloem cells. In *L. noei* the tissue (fig. 4ph) consists at certain points of several layers. The name phloem seems to be appropriate. Hypertrophied cells with darker contents are described by BERTRAND and SEWARD as secretory cells. Polygonal thick-walled cells interspersed at regular intervals are figured by BOWER (2). They have not been recorded from other cones, and according to position and anatomy they are described as pericyclic fibers. Barred cells, occurring on the outer periphery of the xylem, have been observed in *L. oldhamius* (11) and more rarely in *L. bertrandi* (16) but have not been noticed in the other forms here mentioned.

The endodermis, which in recent pteridophytes is markedly differentiated from the other cortical and pericyclic layers, was described and figured by BOWER (2) and ZEILLER (17) for *L. brotenii*. BOWER recognized an endodermis "by the more sharp definition of its walls . . . and the radial walls with characteristic dots" (2). The endodermis BOWER observed was not continuous. ZEILLER indicated tentatively as endodermis a cell layer characterized by distorted zigzag radial walls. He could not follow this sheath around because in many instances the

tissue was decayed (17, pl. II, fig. 8). This wall deformation was the only anatomical character; no wall thickenings or dots were noticed.

Division of the cortex into three parts is in general use. The inner cortex is usually preserved, but if not, the beginning of the internal periphery can be made out by the abaxial projections of the leaf trace, as is seen also in *L. bertrandi* (16) and *L. oldhamius* (1). The nature of the middle cortex as an aerenchymatous tissue, as in *Selaginella*, is well shown in *L. noei*. The lacunar tissue is probably easier attacked and destroyed by decay organisms than the other tissues. The tissue of the middle cortex is continuous into the leaves and laminae as a small strand on the phloem side of the bundle, the parichnos. In different species the development of the parichnos shows in various degrees. In *L. coulteri*, as in other species, it branches at the distal end of the pedicel and accompanies the leaf trace on both sides for a certain distance; in *L. brownii* (17) it terminates in the outer cortex; in *L. noei* almost the same is true; in other forms, as *L. bertrandi* (16), no parichnos is seen at all. The presence of the parichnos seems to be specific. It is not impossible that the degree of its development may reflect the ecological habitat of the specimen.

The sporangia are usually the shape of a five-sided polygon. The sporangium is attached basally to the adaxial side of the pedicel in most forms, or it is median—as in *L. masleni* (3)—at a distance of 1 cm. from the base of the pedicel. The sporangia of *L. noei* are quite long, reaching 20 mm. and being exceeded only by those of *L. masleni* (3), which attain a length of 27 mm. The jacket layer, consisting of an inner and an outer palisade layer, is well differentiated from the tapetal layer in *L. noei*. Owing to early development, the subarchesporial pad extends farther into the sporangium, but later becomes appressed to the floor of the latter, as can be seen by the compressed cells. Probably the growing spores are responsible for this.

Sterile tissue plates have been noticed in *L. oldhamius* and *L. masleni* (in the microsporangia), and their structure is specific. SCOTT (15, Vol. II, p. 165) mentions evidence of sterile tissue in megasporangia but did not illustrate his statement. *L. noei* shows sterile tissue plates also in the megasporangia (fig. 5C). Special enlarged palisade cells at certain points have been described in several forms (such as *L. brownii* and *L. coulteri*). About the function there is no agreement. Two species are known in which the number of megaspores in a sporangium is greater than sixty-four, *L. brownii* (17) and *L. noei*. A comparison of the size of micro- and megaspores within a species shows that the ratio in the homosporous species is 1:1, but varies in the heterosporous species. In *L. bertrandi* it is 1:2; in *L. noei*, 1:5; in *L. brownii*, 1:10; in *L. scottii*, 1:30–40, and in *L. masleni*, 1:45. Phylogenetically *L. masleni* would be considered in this respect highly specialized

and *L. bertrandi* less advanced. Thus a cone may be highly specialized in one respect and primitive in another. The presence of the heel seems to be specific. It is present in most forms but is lacking in *L. noei*. The presence of a ligule is specific for *Lepidostrobus*. It may be inserted in a ligular pit as in *L. arberi* (1) or occur without a ligular chamber.

The structure of the leaf trace is the same in various forms. It is collateral except in *L. oldhamius* (1), where it appears to be concentric at the apex of the sporophyll. The number of xylem elements in the leaf trace varies among the species and may range from nine to as many as seventy. In traversing the axial tissues the leaf trace is accompanied in a peripheral direction by each of the tissue systems through which it passes; for example, a trace passing through the middle cortex is accompanied by phloem, parenchyma, and inner cortical tissue in the immediately peripheral layer. Thus xylem, phloem, parenchyma, etc. are found displaced in a peripheral direction immediately adjacent to the leaf trace.

The sporophylls are arranged in circles or spirals. The data given by ZEILLER (17) show that the phyllotaxy is not constant in *L. brownii*, the number of orthostichies varying from seventeen to thirty-three. In *L. noei* the number is even larger, fifty-one. The partly irregular arrangement of mega- and microsporophylls in *L. noei* seems to be unique. Only by study of additional heterosporous forms can it be determined whether this arrangement of sporophylls is common.

The epidermis is composed usually of thick-walled cells. Some species show a special hypodermal layer.

Summary

1. Two species of *Lepidostrobus* are described, *L. coulteri* Jongmans and a new species, *L. noei* Mathews from Kentucky. Two specimens of the former are described in detail, since nothing was known previously about the structure of the axis of that species. A description and several diagnoses are made on the basis of sections. The size, the presence of a heel, the extension of the leaf traces high into the lamina, together with a well-developed parichnos seem to distinguish these specimens from other described cones. The five cones in the collection suggest a classification among homosporous *Lepidostrobi*.

2. *L. noei*, sp. nov., is unique in that it shows many features not yet observed in other forms. The middle cortex shows the trabeculate structure quite well, although the parichnos does not extend beyond the central portion of the outer cortex. The heel is absent. The cone is heterosporous, the microsporophylls occupying the upper one-third of the cone and the megasporophylls the lower two-thirds. No difference in structure was noticed between micro- and megasporophylls. The ratio in size of the spores is 1:5. The arrangement of micro- and megasporophylls in the same whorl is unusual.

3. A comparison with the hitherto described cones has been made and differences and similarities pointed out. Phylogenetic considerations have been contrasted with the geological appearance of the cones.

The writer is indebted to the late Dr. A. C. NOÉ for suggesting this problem and supplying the material.

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LITERATURE CITED

1. ARBER, A., An anatomical study of the Paleozoic cone-genus *Lepidostrobus*. Trans. Linn. Soc. London 2. Bot. 8: 205-238. 1914.
2. BOWER, O. F., On the structure of the axis of *Lepidostrobus brownii* Schpr. Ann. Bot. 7: 322-354. 1893.
3. CAMPOS, J. D., A new specimen of *Lepidostrobus foliaceus*. BOT. GAZ. 72: 441-449. 1925.
4. COULTER, J. M., and LAND, W. J. G., An American *Lepidostrobus*. BOT. GAZ. 51: 449-453. 1911.
5. ———, A homosporous American *Lepidostrobus*. BOT. GAZ. 72: 106-108. 1921.
6. GRAHAM, R., Pennsylvanian flora of Illinois as revealed in coal balls. II. BOT. GAZ. 97: 156-158. 1935.
7. HIRMER, M., Handbuch der Paläobotanik. Bd. I. München. 1927.
8. JONGMANS, W. J., Fossilium Catalogus. II; Pars 16. Berlin. 1930.
9. ———, Einige Namenänderungen bei *Lepidostrobus*. Geologisch Bureau voor het Nederlandsche Mijngediet te Heerlen Jaarverslag over 1930. Heerlen. 1931.
10. KOOPMANS, R. G., Researches on the flora of the coal-balls from the "Finefrau Nebenbank" Horizon in the province of Limburg (Netherlands). Heerlen. 1928.
11. MASLEN, A. J., The structure of *Lepidostrobus*. Trans. Linn. Soc. London 2. Bot. 5: 357-377. 1899.
12. OGURA, Y., Anatomie der Vegetationsorgane der Pteridophyten. Berlin. 1938.
13. SCOTT, D. H., and JEFFREY, E. C., On fossil plants showing structure from the base of the Waverly shale of Kentucky. Phil. Trans. Roy. Soc. London B. 205: 315-373. 1914.
14. SCOTT, D. H., *Lepidostrobus kentuckiensis*, nomen nov., formerly *Lepidostrobus fischeri* Scott and Jeffrey: a correction. Proc. Roy. Soc. London B. 88: 435-436. 1915.
15. SCOTT, D. H., Studies in fossil botany. Vols. I, II. 3d ed. London. 1920.
16. ZALESSKY, M., Végétaux fossiles du terrain carbonifère du Bassin du Donetz. II. Etudes sur la structure anatomique d'un *Lepidostrobus*. Mém. Comité Géol. St. Pétersb., N.S. Livr. 46. 1908.
17. ZEILLER, R., Etudes sur le *Lepidostrobus brownii*. Mém. Acad. Sci. 52: 1-69. 1911.

